[*From "The Transactions of the Second Entomological Congress, 1912."*]

OBSERVATIONS ON THE CENTRAL AMERICAN ACACIA ANTS.

By WILLIAM MORTON WHEELER, PH.D., BOSTON, MASS.

[*From "The Transactions of the Second Entomological Congress*, 1912."]

OBSERVATIONS ON THE CENTRAL AMERICAN ACACIA ANTS.

By WILLIAM MORTON WHEELER, PH.D., BOSTON, MASS.

THE critics who have recently assailed and even demolished many of the brilliant theories bequeathed to us by the eminent biologists of the latter part of the nineteenth century, have not overlooked the theory of myrmecophilous plants. As originally promulgated by BELT and DELPINO in 1874 and elaborated by BECCARI, HUTH, FRITZ MÜLLER, SCHIMPER, and others, this theory holds that a number of plants, mainly tropical, are protected from their enemies by a body-guard of aggressive ants, and that the plants have been able to enlist the services of these insects by furnishing them with suitable dwellings in the cavities of the stems, leaf-petioles, or thorns, and an unfailing supply of sweet liquid food secreted by the extrafloral nectaries, or of solid food in the form of special bodies containing nutritious oils and proteids. The classical cases which were conceived to place this theory on a firm foundation are the East Indian rubiaceous epiphytes of the genera *Hydnophytum* and *Myrmecodia*, the peculiar neotropical trees of the genus *Cecropia*, and a group of large-thorned acacias peculiar to Central America and Mexico. Other famous cases often cited in this connection are the hollow-stemmed neotropical trees of the genus *Triplaris* and the shrubs of the genus *Cordia*.

TREUB (1888) and RETTIG (1904) have proved that the peculiar cavities in the pseudobulbs of the epiphytic Rubiaceæ have a physiological origin and function quite independent of the ants, which later come to inhabit them, and VON IHERING (1907) and FIEBRIG (1909) have shown that the Cecropias have no more need of the Aztecas, which regularly occupy their hollow limbs and feed on their Müllerian bodies, than dogs have of their

fleas. As the ant acacias seem at first sight to furnish even more irrefutable arguments in favour of myrmecophily, I was glad to have an opportunity during the winter of 1910–11 of studying these plants in several localities in Panama and Guatemala. And although my observations are not as complete as I could wish, I believe they are not without interest, and I feel sure that my sins of omission will be forgiven by any future investigator who spends an equal number of hours in the fierce tropical sun and submits to the fiery stings of an equal number of ants.

It will be remembered that BELT (1874) studied the ant acacias in Nicaragua. He found that the delicate, pinnate leaves of these plants bear crateriform nectaries on their petioles and, when young, also minute, bright yellow food-bodies at the tips of their leaflets. He described and figured the huge stipular thorns, which are paired and connate at the base. They are at first filled with a sweet pulp, which is entirely eaten out of both thorns by the ants, through a single opening made near the tip of one of the thorns, and the smooth-walled cavity thus produced is then used as a formicary. The ants explore the surfaces of the leaves, collect the nectar and food-bodies, and in return for these favours are supposed to protect the plant with their stings from the attacks of herbivorous mammals, and especially from the large leaf-cutting ants of the genus *Atta*. The acacia ants which BELT observed were identified by FREDERICK SMITH as specimens of *Pseudomyrma bicolor* Guérin, which is synonymous with *Ps. gracilis* Fabricius. BELT evidently believed that the ants are in some way responsible for the peculiar enlargement of the thorns.

We now know that the relation between the ants and the acacias had been observed long before BELT'S time. HERNANDEZ (1651) and JACQUIN (1763) both noticed it in Mexico, and COMMELIN figured the food-bodies, or Beltian bodies, as they are now called, as early as 1697, and PLUKENET as early as 1720. Since BELT'S time the acacias have been studied in their native environment only by the Costa Rican naturalist ANASTASIO ALFARO. His observations, however, as reported by EMERY (1891, 1892, 1894), are confined to notes on the various species of ants. All other accounts, such as those of COMMELIN (1697), BECCARI (1884–86), SCHIMPER (1888), and RETTIG (1904), were based

exclusively on herbarium material or on specimens grown in European botanical gardens.

The Species of Acacia and their Distribution.

There seems to be some confusion in regard to the taxonomy of the ant acacias. Recent botanists, following Bentham (1842) distinguish three species, and I believe that they are right in so doing, but I believe that the name of one of them will have to be changed. Bentham cites the species as *Acacia spadicigera* Schlechtendal and Chamisso, *A. sphærocephàla* Schlechtendal and Chamisso, and *A. hindsii* Bentham. I have seen all three of these species growing, but unfortunately my knowledge of *A. sphærocephala* is unsatisfactory, because this species was not in flower during my visit to Central America, and as I was unaware of the peculiarity of its nectaries till after I had consulted the literature and the specimens in the Gray Herbarium, I probably overlooked it repeatedly in the field on account of its close resemblance to *A. spadicigera*. I did, however, see an isolated bush of *sphærocephala* at Las Sabanas, near Panama City, as I have since learned from examining some leaves and thorns preserved in alcohol with the ants. The species known as *spadicigera* and *hindsii* I observed in great numbers, often growing side by side, especially at Escuintla and Patulul in Guatemala. Both species bore fruit, and in a few localities *spadicigera* had begun to blossom. The most striking characters of the three species are the following:

A. spadicigera Schlechtendal and Chamisso is a shrub growing to a height of 10 to 20 feet, often with rather few and diffuse branches. The stipular thorns are large, swollen, gradually tapering towards their tips, and cylindrical or but very slightly compressed at the base. The leaves have a large crateriform nectary at the base of the petiole, and a series of similar but smaller nectaries, each opposite the insertions of a pair of pinnæ. The flower-spike is elongate, clavate-cylindrical, with a thick pulpy peduncle bearing the small, dense flowers. The fruit is thick, spindle-shaped, bright red and leathery when mature, with a long, slender beak, and contains a butter-like, sweetish, edible pulp, in which the black seeds are embedded.

A. hindsii Bentham grows to a larger size than the preceding.

At Zacapa, Guatemala, in the valley of the Motagua River, I saw trees 30 to 40 feet in height. The stipular thorns are large, very broad, usually very much flattened at their connate bases, and suddenly tapering towards their points. The extrafloral nectaries are arranged as in the preceding species. The flower-spikes are also cylindrical, but much more slender. The fruit, too, is more slender and curved, with a shorter beak. When mature it is brown and dry and does not contain an edible pulp.

A. sphærocephala Schlechtendal and Chamisso is a shrub of about the same size as *A. spadicigera*. The stipular thorns are also much as in this species, but usually smaller and of a paler colour. The leaves are furnished with only a single nectary, which is at the base of the petiole. The flower-spikes are globular, the fruit a dry, straight, brown pod, much more slender than in *spadicigera*, and with a short beak or point.

BENTHAM adopted the specific name *spadicigera* and *sphærocephala* because he believed that both of these were included under the *Mimosa cornigera* of LINNÉ (1770, p. 677) and WILLDENOW (1806). On turning to the Systema Naturæ, however, we find that *M. cornigera* L. was based on JACQUIN'S *M. cornigera*, and this author's description clearly rules out *A. sphærocephala*, since the flowers are described as "in spicam aggregantur densam cylindraceam," and the description of the fruits as "coriacea pulpam continent butyraceam" shows that only the species later described by SCHLECHTENDAL and CHAMISSO (1830) as *spadicigera* can be meant. I do not hesitate, therefore, to substitute *A. cornigera* for *spadicigera*, and shall henceforth refer to it only under the former appellation.

It is also possible, I believe, to identify with a reasonable degree of certainty the species of some of the other early descriptions. The earliest of all, that of HERNANDEZ (1651), which he cites under the name *Arbor cornigera* and under the native Mexican name "hoitzmamaxalli," is evidently also *A. cornigera*, since he mentions the "siliquas edules." The species, described by COMMELIN (1697), however, is *A. sphærocephala*, because he says that the flowers are "lutei, numerosi, in globulum, etc.," and that the pods are "fragiles." The species observed by BELT must have been *A. cornigera* and not *sphærocephala*, as SCHIMPER infers (1888, p. 48), because BELT remarks that "at the base of

each pair of leaflets, on the mid-rib, is a crater-formed gland," and the thorns in his figure (1874, p. 218) cannot be those of *A. hindsii*.

The three ant acacias are widely distributed in Central America and Mexico, and *A. spadicigera* is also recorded from Jamaica and the north coast of Cuba.[1] All the species are decidedly tropical and rarely grow above an altitude of 4,000 ft., though they range from Panama to the states of Sinaloa and Tamaulipas in Mexico. In Guatemala and Mexico they are common to both the Atlantic and Pacific littoral, but are absent on the great central plateau. In Nicaragua and Costa Rica the two littoral ranges are, of course, less clearly separated. BELT found *A. cornigera* at Matagalpa in Central Nicaragua, and the same species occurs in Costa Rica as high as Alajuela (about 2,000 ft.), but, according to my observations, does not grow in the immediate vicinity of San José (3,868 ft.), or at Cartago (4,500 ft.).

In this extensive range the three species occupy somewhat different though overlapping stations. *A. hindsii* is known only from Guatemala and Mexico, ranging from near sea-level to somewhat over 4,000 feet. On the west coast of Guatemala, at least, it shows its optimum development at about 600 to 1,200 ft., and specimens are less abundant and more sporadic at higher elevations. It seems to prefer rather dry regions, and

[1] There seems to be some doubt as to the indigenous occurrence of any of the three ant acacias in the West Indies. Prof. N. L. Britton, of the New York Botanical Garden, who has a very intimate acquaintance with the flora of that region, writes me as follows: "As to your Acacia question, I have no definite knowledge of the occurrence of any of the three species you mention in the wild state anywhere in the West Indies, but *Acacia spadicigera* has been found in Cuba by various collectors, apparently always after cultivation, though it is just possible it may be wild somewhere in that island. We have specimens from the vicinity of Havana. I have examined the spines of this Cuban material, but I have found no holes in them, and I myself have never seen the plant living in Cuba."

Brother Leon, of the order of Christian Brothers, whom I recently met in Havana, informs me that he has had under observation a number of *Acacia cornigera* trees in Cuba, and that he has never found ants in their thorns. A number of these, which he kindly forwarded to me, are very large, unperforated, and normal in all respects.

occurs even at Zacapa, a locality noted for its extreme aridity. The two other species require more warmth and moisture, and have therefore a more limited hypsimetrical range. Of *A. sphærocephala* I am unable to speak from much personal observation, but *A. cornigera* will, I believe, be rarely found above an altitude of 1,200 ft. I have already mentioned the fact that it and *A. hindsii* often flourish side by side. This is the case at Escuintla and along the piece of the Panamerican Railway connecting Santa Maria and Patulul. As BELT observed, the acacias do not grow in the forests, but only in the open country or savannahs and along road-sides. They spring up readily in clearings, as one may observe at Quirigua, in the banana plantations of the United Fruit Company. The general distribution of these plants in Central America and Mexico can be inferred from the following list of localities compiled from the literature, and from specimens in the Gray Herbarium and in my own collection :

Acacia cornigera L. (= *spadicigera* Schlechtendal and Chamisso). "Cuernezuela," "Torero," "Palin," "Hoitzmamaxalli."

Colombia : Carthagena (JACQUIN).

Panama : (CUMING) Bentham.

Costa Rica : Alajuela (J. D. SMITH), Gray Herb. ; Nicoya (H. PITTIER), Gray Herb.

Nicaragua : Matagalpa (THOS. BELT).

Guatemala : Escuintla, 1,100 ft. (J. D. SMITH), Gray Herb. ; Escuintla and Santa Maria to Patulul, 413 to 1,111 ft. ; Los Amates, Iguana, and Quirigua (W. M. WHEELER).

Mexico : Cozumel I., Yucatan (Kew Gardens), Gray Herb. ; Merida and Xcholac, Yucatan (C. F. MILLSPAUGH) ; Vera Cruz (HOUSTOUN), Bentham ; Laguna Verde, Vera Cruz (SCHIEDE), Schlechtendal and Chamisso ; San Francisco, near Vera Cruz (C. L. SMITH), Gray Herb. ; Los Cocos, Vera Cruz (A. PETRUNKEWITCH), Amer. Mus. Coll. ; Jalapa (RANGEL), Amer. Mus. Coll. ; Las Palmas, San Luis Potosi (C. G. PRINGLE), Gray Herb. ; Huasteca (L. V. ERVENDBERG), Gray Herb.

Acacia hindsii BENTHAM.

Guatemala : Zacapa and Quirigua, Escuintla and Santa Maria to Patulul, Llano, Palin, Amatitlan, Eureka, 4,686 ft. ;

near San Lucas Toliman, Lake Atitlan 4,000 ft. (W. M. WHEELER); Rio de las Cañas, Punta Rosa, 2,000 ft. (HEYDE and LUX.), Gray Herb.

Mexico: Manzanilla Bay (HINDS), Bentham; Manzanilla, Colima (C. H. T. TOWNSEND), Amer. Mus. Coll.; La Orilla and San Luis between Michoacan and Guerrero (MICHELE), Gray Herb.; Jamiltepec to Rio Verde 400 to 1,000 ft. (E. W. NELSON), Gray Herb.; between Llano Grande and Pinotepa, 200 to 500 ft. (E. W. NELSON), Gray Herb.; Escuinapa, Sinaloa (J. H. BATTY), Amer. Mus. Coll.

Acacia sphærocephala SCHLECHTENDAL AND CHAMISSO.

Panama: Las Sabanas (W. M. WHEELER).

Mexico: Actopan, Vera Cruz (SCHIEDE), Schlechtendal and Chamisso; Vera Cruz to Texas (BENTHAM); Yucatan (G. F. GAUMER), Gray Herb.

OBLIGATORY AND FACULTATIVE ACACIA ANTS.

Just as there are certain species of the dendrophilous ant-genus *Azteca* that live only in *Cecropia* trees, so there are certain species of the equally dendrophilous genus *Pseudomyrma* that live exclusively on the three large-thorned acacias. These I shall call "obligatory" acacia ants. Several other species of the same genus, which are only occasionally associated with these plants, may therefore be designated as "facultative." To the former group belong the three species which EMERY determined, from specimens collected by ALFARO in Western Costa Rica, as *Ps. belti* Emery, *spinicola* Emery, and *nigrocincta* Emery. These species are all of about the same size, but differ in colour, *belti* being black, *spinicola* red, and *nigrocincta* yellow, with a black band across the base of the gaster. I may note in passing that Dr. P. P. CALVERT recently sent me specimens of *Ps. belti* and *nigrocincta*, taken from acacia thorns in Santa Cruz, Guanacaste, Costa Rica. I have taken *spinicola* only in Panama on *A. sphærocephala*. In Guatemala the only obligatory *Pseudomyrmæ* seen on *A. conigera* and *hindsii* are the typical *belti*, and a red subspecies of this ant, *fulvescens* Emery, the former occurring very rarely, the latter on nearly all the trees. In a foot-

note to his paper (1892) EMERY states that the types of *fulvescens* were found by BECCARI in the hollow twigs of *Cordia gerascanthos* in Guatemala, but I believe that this must be a very exceptional occurrence, as *fulvescens* is certainly the most abundant and most typical acacia ant on both the east and west coasts of Guatemala and was taken by me on no other plants. It occurs in two varieties, a larger and a smaller, the former running about with its gaster directed backward in line with the thorax, the latter with the gaster bent forward under the thorax after the manner of *Ps. künckeli* Emery.

BELT mentions only *Ps. gracilis* (= *bicolor*) as occurring in the thorns at Matagalpa, Nicaragua, and as this ant is very common in the hollow twigs of the most various trees and shrubs throughout tropical America, EMERY was inclined to believe that BELT's specimens must have been incorrectly identified by FRED. SMITH. But such a supposition proves to be baseless, since at Quirigua I found a region in the banana plantations where *Ps. gracilis* is the only ant occurring in the acacia thorns. It thus appears that the obligatory ant fauna of the acacias differs in different parts of Central America, although it comprises, so far as known, only four forms: *Ps. belti* and its subspecies *fulvescens*, *Ps. spinicola* and *nigrocincta*. These differences are produced merely by a great local predominance of one or two of the species over the others.

The facultative Pseudomyrmas comprise, so far as known: *Ps. gracilis*, mentioned above; *Ps. subtillissima*, a single colony of which was taken by ALFARO in a tree occupied by *Ps. belti*; and *Ps. nigropilosa* Emery, of which DR. CALVERT sent me a few specimens taken in acacia thorns at Santa Cruz, Costa Rica. We must also assign three other ants of different genera to this group of facultative species; namely the *Crematogaster* mentioned by BELT as living in the thorns of some of the trees in Nicaragua, *Camponotus planatus* Roger, also nesting in the thorns, and a minute yellow *Solenopsis* sp., which I found nesting in the flower peduncles. To the *Solenopsis* and *Camponotus* I shall return after discussing the relations of the obligatory Pseudomyrmas to the acacias.

In Guatemala I found no ants on the dead acacias, which are always abandoned by the obligatory Pseudomyrmas, but ALFARO

was more fortunate in Costa Rica. He sent EMERY the following species taken from the thorns of such trees: *Ps. gracilis* var. *mexicana* Roger, *Ps. nigropilosa* Emery, *Ps. künckeli* Emery, *Crematogaster brevispinosa* Mayr, *Cryptocerus minutus* F., *Cryptocerus* sp. (near *discocephalus* F. Sm.), *Camponotus rectangularis* Emery and *Colobopsis* sp. All or nearly all of these occur in the hollow branches of a great variety of trees and shrubs.

By way of summary I subjoin a list, with localities, compiled from the literature and my collection, of the ten species which are known to occur in the living acacias.

Pseudomyrma belti EMERY.

Costa Rica: Alajuela, Jimenez, Liberia (A. ALFARO); Santa Cruz, Guanacaste (P. P. CALVERT).

Nicaragua: (WM. FLUCK); Grenada (C. F. BAKER); Chontales (FOREL in *Biol. Cent. Amer.*).

Guatemala: Escuintla (W. M. WHEELER).

Mexico: Manzanilla, Colima (C. H. T. TOWNSEND); Escuinapa, Sinaloa (J. H. BATTY); Acapulco (C. F. BAKER); Orizaba (H. DE SAUSSURE).

Ps. belti fulvescens EMERY.

Colombia: Sabanilla (C. GAGZO).

Nicaragua: Grenada (C. F. BAKER).

Guatemala: Zacapa, Quirigua, Escuintla, Patulul (W. M. WHEELER); Champerico (FRED. KNAB).

Mexico: Santa Lucrecia, Vera Cruz (FRED. KNAB); Cordoba (FRED. KNAB); Los Cocos, Vera Cruz (A. PETRUNKEWITCH); Jalapa (RANGEL); Tampico (H. JOURDAN); Torola, Chiapas (A. PETRUNKEWITCH).

Ps. spinicola EMERY.

Panama: Las Sabanas (W. M. WHEELER).

Costa Rica: Alajuela, Jimenez, Pozo Azul (A. ALFARO) Subures near San Mateo.

Nicaragua: Chontales (JANSON).

British Honduras: Belize and Manatee (J. D. JOHNSON).

Mexico: Teapa, Tabasco (H. H. SMITH); Acapulco (FRED KNAB).

Ps. nigrocincta EMERY.

Costa Rica : Alajuela and Jimenez (A. ALFARO) ; Santa Cruz, Guanacaste (P. P. CALVERT).

Ps. nigropilosa EMERY.

Costa Rica : Santa Cruz, Guanacaste (P. P. CALVERT).

Ps. gracilis FABR.

Guatemala : Quirigua (W. M. WHEELER).

Ps. subtillissima EMERY.

Costa Rica : Alajuela (A. ALFARO).

Crematogaster SP.

Nicaragua : Matagalpa (BELT).

Solenopsis SP.

Guatemala : Escuintla (W. M. WHEELER).

Campanotus planatus ROGER.

Guatemala : Costa Rica (A. ALFARO) ; Zacapa, Quirigua, Escuintla, and Patulul (W. M. WHEELER).

THE HABITS OF THE OBLIGATORY PSEUDOMYRMAS.

As BELT observed, the stipular thorns of the acacias are at first rather soft and green, and contain a watery, sweetish pulp. Only after they reach their full size and shape do the ants pay any attention to them. Then the insects select a spot near the tip of one of the thorns of each pair, make an elliptical hole in the cortex, and dig out the pulp. I am not sure that the ants eat this pulp, as BELT implies, but this is not improbable, considering its sweet taste and the large amount of water it contains. After one thorn is hollowed out, the excavation is carried through its base into the adjoining one, which is also reduced to a mere shell. All the particles excavated from both thorns are carried out through the single orifice, and one almost never sees a pair of thorns with an opening near the tip of each. During or just

after the process of excavation the cortex and tips of the thorns harden and turn brown, and the ants take up their dwelling in the hollow structure. A single branch may display in sequence the various stages in this excavation and habitation, the old thorns at the base being filled with ants and their brood, the more distal thorns completely hollowed out, and only just tenanted, and the green thorns at the tip of the branch still intact or with merely the beginnings of an aperture or a small excavation in the pulp itself.

It occasionally happens that the ants overlook thorns which have reached the right stage for excavation. These nevertheless mature and turn brown exactly like the inhabited thorns, and when cut open are seen to have become hollow through a drying up of the pulp. It is evident, therefore, that unless the ants utilise the pulp as food, they are really wasting their time and energy in excavating the green thorns, since they would achieve the same results much more easily by boring through the cortex of old thorns. They would then merely have to remove the few fibrous remnants of the pulp, and the thorns would be ready for habitation. Such behaviour would, of course, require a greater initial effort in perforating the harder cortex of the old thorns.

The structure of the Beltian bodies has been carefully studied by MENEGHINI and SAVI (1884), FRANCIS DARWIN (1877), and SCHIMPER (1888), who all agree in regarding these peculiar structures as the homologues of the serration-glands on the leaf-borders of many other plants. At first I had some difficulty in finding the Beltian bodies, because I looked for them on large trees, from which they had been removed by populous colonies of ants; but later I detected them readily. Only on one occasion, however, was I fortunate enough to see the ants in the act of collecting them. This was while I was walking in the outskirts of Patulul, along a road which was bordered with a hedge of *Erythrina* trees. Among these stood two *A. cornigera* bushes, about 8 ft. apart, with their trunks connected by barbed wires, along which were passing processions of *Ps. fulvescens* workers, each bearing a minute yellow body in its mandibles. Closer inspection showed that one of the trees was peopled by a large colony of Pseudomyrmas, and that they had just discovered, on the young leaves of the other uninhabited tree, an abundant

supply of Beltian bodies, which they were now busily plucking and carrying home, over the barbed-wire bridges, to their nests in the thorns. Later I found that the Beltian bodies are, as a rule, so eagerly sought and so quickly removed from the young leaves of trees inhabited by vigorous colonies, that none of these structures is to be found on the leaflets by the time they unfold.

The liquid food-supply is derived by the ants from the extra-floral nectaries on the upper surface of the leaf-petioles, and in all probability also from the pulp in the young thorns. As in other plants, the nectar is produced most abundantly on the young leaves and in the early morning, so that the ants are most assiduous in collecting the supply at this time, though some of them may be seen exploring and licking the dry surfaces of the nectaries and visiting other parts of the leaves, both old and young, at all hours of the day.

Shaking or roughly touching the branches at once excites the ants. The shock itself, or possibly some stridulatory signal emitted by the insects that first feel the shock, is transmitted to the ants in the thorns. Without a moment's hesitation the angry creatures issue from the small elliptical apertures, rain down upon the intruder, and thrust their burning stings into his flesh. While stinging the *Pseudomyrma* curves its body in an arc and bites with its mandibles at the same time, often persisting in this position till it is torn away from the skin. The pain thus produced is considerable and may endure for hours, though it is confined to a very limited area. The sting of *Ps. spinicola* is somewhat more painful than that of *Ps. belti* or its subspecies *fulvescens*.

The foregoing observations agree very closely with BELT'S, and certainly at first sight suggest an intimate symbiotic relationship between the ants and the acacias. There is, of course, nothing remarkable in the ants' utilising the nectar and food-bodies, because almost any dendrophilous ants would do this, but the uniform and purposeful method of excavating and inhabiting the thorns certainly implies a singular degree of familiarity with the suitability and consistency of these structures. But the matter assumes a different aspect when we consider *Ps. gracilis*. This ant, which is highly variable in colour and one of the largest and most abundant species of the genus throughout

tropical America from Brazil to Southern Texas, nearly always nests in hollow twigs and shows merely local preferences for certain kinds of trees and bushes; but in Nicaragua, where BELT made his observations, and in one locality in Quirigua, Guatemala, as previously stated, this ant has taken to nesting in the acacia thorns. It hollows these out in precisely the same manner as do the regular *Pseudomyrmæ*, making the aperture at the same point near the tip of one thorn of each pair. The aperture, however, is larger because it has to admit larger ants, and for the same reason it takes very few *gracilis* workers, larvæ, and pupæ, to fill the cavity of a pair of thorns. Such rapid and perfect adaptation on the part of *Ps. gracilis* indicates that no special hereditary instinct modification may have been required to induce the same adaptation in *Ps. belti*, *spinicola*, and *nigrocincta*, for these three species, like *gracilis* and many other *Pseudomyrmas*, very probably once nested in all kinds of trees.

BELT'S observations, however, suffer from an erroneous supposition and an important lacuna. After correctly describing the way in which the ants hollow out the thorns, he says (1874, p. 221): "Strange to say, this treatment seems to favour the development of the thorn; whilst in my plants that were not touched by the ants, the thorns turned yellow and dried up into dead but persistent prickles. I am not sure, however, that this may not have been due to the habitat of the plant not suiting it." This cautious statement in regard to the enlargement of the thorns becomes a very positive one in BECCARI'S account of the ant acacias (1884–86), where he says: "Mi sembra indubitato che tale maggiore rigonfiamento debba attribuirse alla irritazione prodotta dalle formiche." He reached this conclusion, which has also been repeated by more recent writers, from finding that the thorns of *A. cornigera* grown in Italy, and therefore free from ants, were less curved and dilated at the base than the thorns of some herbarium specimens that had been inhabited by ants. It never occurs to him that the thorns may be highly variable, even on the same tree, as indeed they are; just as it seems never to have been observed by BELT that a certain number of thorns often remain small and turn yellow even on large, healthy trees. This, together with the fact recorded above, that the thorns are entered by the ants only after they have attained

their full size and characteristic shape, or at any rate at once cease growing and turn brown as soon as they have been hollowed out, suggests an interesting question as to the true cause of the enlargement of the thorns.

The important lacuna in BELT's account is the lack of any observations on the first invasion of the young acacia by the ants. That he endeavoured to answer this question, but failed, is clear from the following quotation: "I sowed the seeds of the acacia in my garden, and reared some young plants. Ants of many kinds were numerous; but none of them took to the thorns for shelter, nor the glands and fruit-like bodies for food; for as I have already mentioned, the species that attend on the thorns are not found in the forest. The leaf-cutting ants attacked the young plants and defoliated them, but I have never seen any of the trees out on the savannahs that are guarded by the *Pseudomyrma* touched by them, and have no doubt the acacia is protected from them by its little warriors."

It is regrettable that BELT failed to observe seedling acacias in their native savannahs, for had he done so he might have modified his views in regard to the myrmecophily of these plants. But seedling acacias are rare even where the bushes and trees abound. Quirigua was the only locality in which I succeeded in finding them, probably because the dry season was prevailing in all the other places I visited in Guatemala. In the clearings that were being made for the banana plantations, I found many young plants of *A. cornigera* between 8 in. and 2 ft. in height. Several of these, though vigorous and almost in the very paths of large colonies of leaf-cutters, were nevertheless perfectly free from Pseudomyrmas. The thorns of others, however, contained isolated, recently fecundated queens of *Ps. fulvescens* or *Ps. gracilis* in the act of establishing their colonies. Brief descriptions, drawn from my note-book, of two of these plants will suffice. One, only 8 in. high, bore but a single pair of thorns, which were hollow and contained a solitary deälated queen of *Ps. fulvescens*. She had made the typical opening near the tip of one of the thorns, and was evidently waiting for the eggs to mature in her ovaries. Another plant, 14 in. high, was more interesting. It bore 5 pairs of thorns, each of the three basal pairs of which was inhabited by a deälated queen; the two

distal pairs were green and still intact. The queen in the lowermost pair was guarding a few larvæ and pupæ; the two others had as yet produced no young, and, curiously enough, the orifices through which they had excavated and entered the thorns had grown over and closed, though their position was still marked by a scar on the outside. This closure, which I observed also in some of the other seedlings, recalls the conditions in *Cecropia*, each young internode of which is perforated by the *Azteca* queen at a preformed pit, which then closes over by the growth of the plant, so that the insect is imprisoned till the wall is again perforated at the same spot, but from the inside, by the worker brood, and the young colony establishes its communication with the outside world.

It is evident, therefore, that it is the queen *Pseudomyrma* that attaches the ant colony to the acacia, by a type of behaviour which is merely repeated by her offspring when they hatch and enlarge the colony by excavating and moving into additional thorns as fast as these mature on the more terminal portions of the trunk and branches. My observations also show that even when the seedling acacias grow in localities where the leaf-cutting Attas abound, they cannot be protected by the *Pseudomyrmæ* till they are more than a foot high, for the queens do not leave their thorns, since they are at this period as timorous as all young isolated ant queens. Moreover, the closure of the openings of the thorns would prevent many of them from defending the plants, even if they were so inclined.

A more difficult question is that relating to what must occur when the young broods, produced by the various queens that occupy successive thorns, come forth on to the surface of the plant in search of food. Do these broods fight with one another till only one and its queen survive, as VON IHERING believes to be the case among the *Cecropia* Aztecas? Or do the various broods fraternise and fuse to form a single, large, polycladic colony? I am unfortunately unable to decide between these alternatives, but I am inclined to believe that the various broods unite, and that the thousands of ants which occupy all the thorns on a single tree represent a colony which arose by a coalition of the broods of all the queens that peopled the few available thorns on the very young plant *plus* the broods that have been produced

by the daughters of these queens moving into thorns on the same tree as fast as these became suitable as dwellings. That different colonies of the same species of *Pseudomyrma* may thus readily coalesce is also indicated by the fact that these ants so readily tolerate the presence of certain other distantly related species on the same tree, as I shall now proceed to show.

The Cases of Parabiosis.

It is usually supposed that only one species of ant occurs on an acacia tree, but we have seen that Alfaro on one occasion found both *Ps. belti* and *subtillissima* living side by side, and this observer also found a second ant, *Camponotus planatus*, on trees inhabited by the *Pseudomyrmas*. Emery's account of these observations is not altogether clear. He seems to imply that the *Camponotus* is merely a "Raumparasit," or inquiline of the *Pseudomyrma*, and that it prefers to occupy the thorns of the dry or dead branches. *C. planatus* is, according to my own observations, one of the most abundant neotropical ants, and has much the same distribution as *Ps. gracilis*. Like this ant it usually nests in the hollow twigs of a great variety of trees and bushes. It is timid and very rapid in its movements, and in its foraging and feeding habits resembles the other small arboreal species of the huge genus *Camponotus*. I was surprised, therefore, to find this ant on a large proportion of the living *A. cornigera* and *hindsii* bushes at Escuintla, Patulul, and Quirigua, in company with *Ps. fulvescens*, which it resembles in colour though not in form. I was still more surprised to find it associated in the same manner with the large black *Ps. gracilis* at Quirigua, where this ant has become a common acacia tenant. In all of these localities and, as I have said, in many of the trees, a large number of the thorns were occupied by *C. planatus*. And these thorns were on the same twigs and branches as those occupied by *Ps. fulvescens*. The thorns containing the *Camponotus* are easily recognisable, for they have larger openings because the body of this ant, though shorter, is stouter than that of the *Pseudomyrma*.

That the *Camponotus* does not, as Emery supposed, merely take possession of thorns excavated and abandoned by the *Pseudomyrma*, was proved on one occasion when I found a small

group of *Camponotus* workers busily engaged in perforating a green thorn. It is probable, therefore, that the *Camponotus* queens, after their nuptial flight, seek out the acacias and enter their young thorns even when the trees are already inhabited by the *Pseudomyrma*, and that the *Camponotus* workers continue this work side by side with the *Pseudomyrmæ*, both species competing for and taking possession of the thorns as fast as they attain the proper size and maturity. It is certainly extraordinary that *C. planatus*, which throughout tropical America so constantly lives in hollow twigs, should be able in widely separated localities to utilise the acacia thorns as perfectly and in precisely the same manner as the regular Pseudomyrmas. That the *Camponotus* is, if anything, even more adroit in its use of the extrafloral nectaries becomes apparent when one follows the ant as it moves over the leaves, for it begins with the nectary at the base of the petiole and carefully visits each in turn, whereas the foraging Pseudomyrmas are much more desultory and less businesslike. I have not seen the *Camponotus* collecting the Beltian bodies, but I doubt not that they make quite as good use of them as of the nectar.

The behaviour of the two species of ants towards each other is peculiar. They seem never to quarrel, and, if not too close together, pass one another on the twigs and leaves with an air of complete indifference. But when two of them happen to meet squarely face to face, each starts back suddenly and, curiously enough, the *Pseudomyrma* always recoils more vigorously than the *Camponotus*. There is something ludicrous in this behaviour, because both ants are of about the same bulk, and the *Pseudomyrma* is really the more powerful and possesses a formidable sting, whereas the *Camponotus* is much less pugnacious and can defend itself only with its rather feeble mandibles and formic acid battery. But it smells rather strongly of formic acid, and I believe that this produces the more decided reaction on the part of the *Pseudomyrma*.

Still another ant which I found repeatedly nesting in *A. cornigera* bushes with *Ps. fulvescens* in a pasture near Escuintla, Guatemala, is a minute yellow *Solenopsis*, which seems not to have been described. Its small colonies were not nesting in the thorns, but in the old spindle-shaped flower-peduncles from which

the ripe fruit had fallen. The ants had converted each peduncle into a nest by providing it with a small circular opening, and removing the pulpy tissue from its interior. In all these nests, and attached to their walls, were several small reddish Coccids, the excrement of which is probably an important part of the ant's food. I did not see the *Solenopsis* out on the stems and foliage, but even if they are in the habit of frequenting the surfaces of the plant, they are probably completely overlooked by the *Pseudomyrmæ* on account of their minute size. Similar small yellow species of *Solenopsis* (*S. fugax* Latr., *S. molesta* Say, etc.) are known to live in the walls of the earthen nests of various European and North American ants and to prey on their larvæ and pupæ. It would be interesting to know whether the acacia *Solenopsis* ever assumes a similar lestobiotic relation towards *Ps. fulvescens*.

I believe that we may regard the relationship existing between *Ps. fulvescens* and *gracilis* on the one hand, and *Camponotus planatus* on the other, as one of parabiosis. This term was first introduced by FOREL in 1898 to designate a peculiar pacific relationship between *Dolichoderus debilis* and *Crematogaster parabiotica*. He found these two ants in Colombia nesting in an abandoned termite nest, in such a manner that each species kept its brood together in its own chambers and galleries, but the chambers and galleries of the one species interdigitated and even inosculated with those of the other in a very intimate manner. The two species, moreover, foraged together on the same plants, either separately or in a common file. Each of them was also found nesting by itself. I may say in passing that I found no less than a dozen colonies of these same ants in Panama and Guatemala, and in all cases their nests presented essentially the same peculiarities as those described by FOREL. Their foraging habits, too, conformed with his description. MANN (1912) has very recently described similar parabiotic relations between certain Brazilian ants (*Dolichoderus bispinosus* Oliv. and *Crematogaster* sp.; *Odontomachus affinis mayi* Mann and *Dolichoderus debilis* var. *rufescens* Mann). Some years ago I also included under the head of parabiosis the cases in which different species of neotropical ants show a tendency to inhabit the same Tillandsias and other Bromeliaceous epiphytes. To these various

cases may now be added the association of *Ps. belti* with *Ps. subtillissima*, and of *Ps. fulvescens* and *gracilis* with *C. planatus*.

Other Organisms Associated with the Acacias.

It is probable that other insects besides the ants occasionally visit the extrafloral nectaries of the acacias. Belt states that these organs are "frequented by a small wasp (*Polybia occidentalis*)." But besides the ants and the Coccids mentioned above as living in the hollow flower peduncles of *A. cornigera*, I saw only the following insects or evidences of their occurrence on the plants:—

1. In some localities (Escuintla, Patulul) the upper surfaces of the pinnæ of *C. cornigera* bore beautiful little spherical galls, 5 to 6 mm. in diameter, singly or in clusters, and resembling minute strawberries, as they were bright red and uniformly covered with papillæ. Each of these galls contains a Dipteran (Cecidomyiid ?) larva and has a preformed rhaphe along which it dehisces when brown and mature, and permits the adult fly to escape. *Ps. fulvescens* is very fond of visiting these galls when young and succulent, and was often seen gnawing away the covering of papillæ, but not eating in far enough to injure the enclosed larva.

2. A second gall of larger size and woody texture was occasionally seen on the flower stems of *A. hindsii*, but as I saw only old and dried specimens, I am unable to make any statement in regard to the insect.

3. The brilliant yellow flower spikes of *A. cornigera* are pollinated by small bees which resemble some of our northern species of *Halictus*.

4. On some of the acacia trees and bushes I found the paper nests of various species of *Polybia*, some deserted, but others still occupied by the wasps.

5. Along a road near Escuintla I found several young acacias wholly or in part defoliated, though their thorns were still teeming with *Ps. fulvescens*. There were no leaf-cutters in the vicinity, and the defoliation was not of the type characteristic of these ants, but resembled that of certain caterpillars or Chrysomelid beetle larvæ.

Finally I may mention that I occasionally found well-constructed but abandoned birds' nests in the acacias. If these at some former period really contained young birds, it is difficult to see how these could have escaped being molested by the Pseudomyrmas.

The Ant Acacias of South America and Africa.

Since Belt described the Central American acacias, species with similar relations to ants have been discovered in South America and Africa, and as these are not without interest in connection with the foregoing observations, I may be pardoned for briefly discussing them.

South American ant acacias are known only from Paraguay. In 1896 Emery enumerated the following series of ants as having been found by Dr. J. Pohls nesting in the robust, wooden thorns of a species of Acacia in that country: *Pseudomyrma acanthobia* Emery, *Leptothorax spininodis* Mayr, *Cryptocerus pusillus* Klug, *pilosus* Emery, *bohlsi* Emery, *peltatus* Emery, *quadratus* Mayr, *pallens* Klug, *grandinosus* F. Smith, *Crematogaster brevispinosa* Mayr, and *Myrmelachista nodifera* Mayr var. *flavicornis* Emery. Most of these species seem merely to excavate galleries in the woody tissue of the thorns, without hollowing them out after the manner of the Central American ants. *Ps. acanthobia* perforates the thorns near the tip, the other species nearer the base. The latter often make several openings in the same thorn.

Much more like the conditions in the Central American acacias are those recently described by Fiebrig (1909) for *Acacia cavenia* H. and A. of Paraguay. The pairs of thorns on this tree are often greatly enlarged and are frequently inhabited by an ant, *Ps. fiebrigi* Forel, which makes its opening near the tip of one of the thorns. Fiebrig found that the thorns are often hollowed out by a Tineid larva, and he believes that the cavities thus formed are later appropriated by the *Pseudomyrma*. No Beltian bodies were found on the few plants on which they were sought, and no mention is made of the extrafloral nectaries. The acacia grows only in low grounds which are occasionally flooded, and where there are no leaf-cutters.

Even more interesting are the East African ant-acacias which

have been studied by KELLER (1892), and more recently and somewhat more closely by SJÖSTEDT (1908). These acacias are *A. fistula* Schweinf., *zanzibarica* Taub., *drepanolobium* Harms, *seyal* Del., and *bussei* Harms. Their stipular thorns exhibit a much greater variety of shape and a much more extraordinary enlargement at the base than is found in any of the American species. So extreme is this enlargement, in fact, that SJÖSTEDT regards them as galls, and believes that they may owe their development to the stings of Diptera or Hymenoptera or, more probably, to the irritation produced by certain Coccids which he found on the very young twigs. Both KELLER and SJÖSTEDT, however, are certain that the ants have nothing to do with the modification of the thorns, since they found them attaining their full size before being entered by the ants, and also on bushes that harboured none of these insects. The galls are at first solid and are hollowed out by the ants. These belong mostly to the dendrophilous genus *Crematogaster*. The species taken in the thorns of *A. fistula* by KELLER and identified by FOREL (1892) were *C. chiarinii* Emery, *acaciæ* Forel, and *ruspolii* Forel. SJÖSTEDT took *C. chiarinii* in the thorns of *A. zanzibarica*; *C. admota* Mayr, *C. sjöstedti* Mayr, and *Sima penzegi* Mayr in those of *A. drepanolobium* and *C. solenopsidis* Emery var. *flavida* Mayr and *Cataulacus intrudens* F. Sm. in the thorns of *A. bussei*. The various *Crematogasters* do not perforate the tips of the thorns, like the Pseudomyrmas, but make one or more round holes in the dilated basal or gall portion. It may be noticed in passing that the *Crematogaster* which BELT found nesting in *A. cornigera* has the same habit. The African acacias bear no Beltian bodies, although they are furnished with crater-shaped nectaries on the leaf-petioles. SJÖSTEDT failed to observe the ants in the act of visiting these nectaries, but he admits that they may do so when the leaves are very young. One infers from his description that the ants obtain their food largely from the numerous Coccids (*Dactylopius coccineus* Newst.) and larval Membracids which infest the plants. Both KELLER and SJÖSTEDT believe that these acacias of the African plains may be protected from the antelopes, goats, and camels by their ants, although these are certainly far less vicious than the American Pseudomyrmas. It is, however, by no means clear that the plants are

not sufficiently protected by their long, sharp thorns from the browsing animals.[1]

Are the Acacias Myrmecophilous?

After presenting all the essential facts, so far as known, concerning the acacias and their ants, we are prepared to consider the question as to whether these plants are actually myrmecophilous, as implied in the Belt-Delpino hypothesis. In other words, have these plants developed their extraordinary thorns, extrafloral nectaries, and Beltian bodies for the purpose of insuring the presence of a body-guard of stinging ants? It is certain that acacias that are quite free from ants grow and flourish quite as well as ant-infested individuals, and produce the thorns, nectaries, and Beltian bodies in a perfectly normal manner. This I have found to be the case in a few localities in Western Guatemala, and also, under interesting circumstances, in the banana plantations about Quirigua. In the latter locality the negroes, while making clearings, had carefully lopped off all the branches of many of the old acacias, leaving only their stumps. These had then put forth vigorous young branches, which, however, were quite free from ants, evidently because they had grown out, and their spines had matured at a time when the recently fecundated *Pseudomyrma* queens were not flying about in search of nesting sites. Finally, attention may be again called to the fact that the very young acacias, which would seem to require the greatest amount of protection, are either entirely free from ants, or contain only young queens hidden away in the hollow thorns.

[1] Since the foregoing paragraphs were written, Dr. Glover Allen, of the Boston Society of Natural History, has, at my request, made some interesting observations on the enlarged thorns of *Acacia fistula* in the Blue Nile and Dinder River Valley, while accompanying Dr. J. C. Phillip's Sudan Expedition. On cutting open very young thorns, which were only slightly swollen at the base, he found them to consist "of a solid mass of green, succulent tissue, with a single small larva inside, as in a typical insect gall." This larva seemed to be that of some Hymenopterous insect. His observations, which will be published in detail later, show very clearly that the enlarged thorns are not only galls, which are formed independently of the ants, as Sjöstedt observed, but that these structures are inhabited by very few ants during January and February.

The Belt-Delpino hypothesis clearly implies that unless protected by the Pseudomyrmas the acacias would be destroyed either by the browsing cattle or by the leaf-cutting ants. Yet it must be evident at once, to any one who sees these plants growing in the savannahs of Panama and Guatemala, that their thorns alone would protect them from the attacks of horses and cattle, for these thorns are not weak or ineffective, as some writers seem to imagine, but are, as RETTIG says, at least as formidable as the thorns of many species of hawthorn (*Cratægus*). I should say that they are even more formidable than any of the thorns I have seen on the numerous hawthorns growing in the Arnold Arboretum.

Most authors, however, dwell more on the leaf-cutting ants of the genus *Atta* as the principal enemies of the acacias. BELT'S seedlings were destroyed by these pests, and I willingly admit that a similar fate may occasionally overtake these plants in Guatemala, although I never saw one attacked, even in Quirigua, where both seedlings and older bushes grow in the clearings near the large *Atta* formicaries, and almost in the beaten paths of the ants. In other localities, such as Zacapa and Patulul, I was often unable to find leaf-cutters in any part of the extensive areas occupied by the acacias. From my observations on these ants in Panama, Costa Rica, Guatemala, Mexico, and Texas I am convinced that their rôle as destroyers of plant-life has been grossly exaggerated, and VON IHERING and FIEBRIG have acquired the same conviction from their observations in Brazil and Paraguay. The Attas do, indeed, occasionally defoliate trees or shrubs, but they are not sufficiently numerous to do this over any considerable area, nor so thoroughly and repeatedly as to endanger the existence of any native plant species. That they often destroy introduced or cultivated plants, such as rose bushes, is true, but these are grown in small, compact cultures, and are not scattered over immense stretches of country, much of which is always quite free from *Atta* colonies. I conclude, therefore, that the existence of the acacias as species is very far from being endangered by the leaf-cutters. What, then, are the great destroyers, against which such a body-guard of stinging ants has to be levied, garrisoned, and fed by the acacias? As nobody is able to tell us, are we not justified in casting the *onus*

probandi of myrmecophily on the shoulders of him who affirms its existence ?

But when answered in this manner, the advocate of myrmecophily shifts his ground and says that the acacias have obviously survived a multimillennial struggle with enemies which are now either much reduced in numbers and hostility, or have altogether perished, and that it was during this struggle that the plants were compelled to hold out inducements to an emmet body-guard, which is perhaps at the present time nothing more than a useless survival. Such arguments, in the face of our complete ignorance of the past history of the ant acacias, may be passed over without comment, or by merely pointing to the fact that there are in Central America and Mexico many other species of *Acacia* and acacia-like plants, with equally delicate foliage, and growing in the same localities, but without enlarged thorns, extrafloral nectaries, food-bodies, and attendant ants. Why have these more numerous and more defenceless species survived without the assistance of the Pseudomyrmas ?

I admit that the thorns, extrafloral nectaries, and food-bodies are peculiar structures requiring an explanation. But such an explanation should first be sought along physiological lines. Madame VON ÜXKÜLL-GÜLDENSTERN (1907) has recently shown that botanists are still as ignorant as they were in the days of LINNÉ in regard to the function of the extrafloral nectaries of plants in general. And the significance of such structures as the Beltian bodies of the acacias, the Müllerian bodies of the Cecropias, and the " bead-glands " of these and many other tropical plants rarely or never visited by ants, is even more obscure. The extraordinary enlargement of the thorns of the ant acacias, especially of the African species, in which they are sometimes so voluminous that the Crematogasters have to construct carton partitions across their cavities, in order to convert them into suitable nests, also suggests that these organs have some unknown significance in the life of the plant, quite apart from their suitability as dwellings or as supplies of food for the ants.

The whole matter becomes clearer, I believe, when we turn to the acacia ants themselves, for there can be no doubt that these are exquisitely adapted to the plants. We have seen that four of the Pseudomyrmas occur in no other situations, and that they

are perfect adepts at utilising the thorns as dwellings, and the nectar and Beltian bodies as food. The simplest explanation, therefore, is that these ants were formerly pandendrophilous, like the vast majority of *Pseudomyrma* species, but that they long ago discovered the greater advantage of living on the acacias, and have since confined their attention exclusively to these plants. That this adaptation may have been very easily and quickly established is shown by *Ps. gracilis* and *Camponotus planatus*, both widely distributed, and pandendrophilous ants, which in certain regions have become as completely adapted to the acacias as the obligatory Pseudomyrmas. On this view there is nothing any more remarkable in the predilection of particular ants for particular species of plants than there is in the predilection of particular phytophagous insects for particular host plants. Indeed, this view can be rejected only by those who are unfamiliar with the ant-life of the tropics, who have never been impressed by the vast numbers of these insects perpetually exploring the surfaces of the rank and varied vegetation in their eager search for food and habitations. No suitable cavity in the plant body, no sweet exudation, no particle of accessible food escapes their attention, and any plant that furnishes one or more of these desiderata is at once appropriated and becomes "myrmecophilous." And although it must be admitted that some of these dendrophilous ants (*Pseudomyrma, Azteca*) sting and bite severely, and may therefore defend the plants, this is, of course, merely a coincidence or by-product, as it were, of the true defence which the ants exercise in behalf of their own bodies and their brood. I believe, therefore, that we may adopt VON IHERING'S point of view, and say that *Acacia cornigera, hindsii,* and *sphærocephala* have no more need of their ants than dogs have of their fleas. If this is true, the relation between the ants and plants is not one of symbiosis, but one of parasitism.

NOTES ON CENTRAL AMERICAN SPECIES OF CECROPIA AND TRIPLARIS.

The case of the acacias is, indeed, much more like that of the Cecropias than is generally supposed. Some years ago (1907)

I showed that in Porto Rico a common tree of this genus (*C. peltata*), though fully equipped with the so-called myrmecophilous adaptations (*i.e.* the hollow stems, internodal prostomia, and Müllerian bodies), is never tenanted by Aztecas, because there are no Aztecas on the island, nor, in fact, on any of the larger Antilles.[1] It is also known that some of the Brazilian Cecropias are free from these ants. Several species of *Cecropia* (*C. humboldtiana* Klotzsch, *insignis* Liebm., *obtusifolia* Bert., *polyphlebia* Don. Smith, *mexicana* Hemsl., and its variety *macrostachya* Don. Sm.) occur throughout Central America up to altitudes of about 3,500 ft. Some of them are really tree-weeds, which spring up in great numbers, like their herbaceous allies, our northern nettles, in all clearings. After examining hundreds of young and old trees I have come to essentially the same conclusions as VON IHERING and FIEBRIG. As young trees 3 to 6 ft. in height, the Cecropias contain only isolated queen Aztecas in their hollow internodes, just as the young acacias contain only isolated *Pseudomyrma* queens in their thorns, and are therefore quite as defenceless as other plants which have no thorns or stinging hairs. Nevertheless these young Cecropias are very rarely attacked by the leaf-cutters, and their foliage is really in much better condition than that of the older trees, in which the queens have produced hordes of belligerent workers. The foliage of such old trees is often much eaten by sloths, caterpillars, and Chrysomelid beetles or their larvæ, as has also been noticed by the observers in South America. On one occasion at Gatun, in the Canal Zone, I saw a female sloth, with a young one on her breast, leisurely devouring the large palmate leaves of a tall, ant-infested *Cecropia*. The foliage of this tree seems, in fact, to be the favourite food of these extraordinary mammals. FIEBRIG has also described complete defoliation of Cecropias in Paraguay by grasshoppers. These few notes will suffice to show that the famous case of these plants is no more clearly established in favour of the Belt-Delpino hypothesis than is that of the acacias.

[1] Recently I have made the same observation on the Cecropias which abound in the hilly regions of the provinces of Havana, Matanzas, and Santa Clara, Cuba. These trees, though closely resembling the continental species of the genus in the structure of the internodes, trichilia etc., have no ant inhabitants.

The species of the Polygonaceous genus *Triplaris* are also included among the "myrmecophilous" plants, although they are not known to bear extrafloral nectaries or food-bodies, and merely accommodate the ants with dwellings in their hollow stems. Some of the species are said to have bright red flowers, and either for this reason, or because one can hardly touch the trees without being stung by the ants, are widely known in tropical America under the name of "palo santo."

I was able to study one of the species of *Triplaris* (*T. cumingiana* Fisch. and Mey.) through the kindness of Mr. Christophersen, who guided me to several specimens growing in low, marshy ground at Frijoles on the old line of the Panama Railroad. These trees were 15 to 20 ft. high, with very slender trunk, smooth, light grey bark, and long, narrow, lanceolate leaves. When the trunk was cut down and split longitudinally, it was seen to have a very slender cavity in the centre and extending its full length, and communicating with a similar slender cavity in the centre of each branch. This continuous system of cavities communicated with the surface by numerous slender galleries, excavated by the ants, and terminating in small round orifices, which served as exits and entrances. Each tree was occupied by a single large colony of *Ps. arboris-sanctæ*, a yellow species, which is larger and stings more severely than the regular acacia Pseudomyrmas. As the *Triplaris* trees were isolated, and as their bases must stand in the water during the rainy season, it is difficult to understand how the ants manage to exist, unless they remain rather dormant during this season or find some hitherto unknown food-supply on the foliage.

A second and very different species of *Triplaris* (*T. macombii* Don. Smith) was seen in great numbers along the beautiful roadsides of Patulul and Escuintla in Guatemala. This is a larger tree, often attaining a height of 30 to 40 ft., with more diffuse branches and large, coarse, ovate leaves. Early in January it began to put forth bunches of long, yellowish flower-spikes, which were covered with a deciduous sheath. The branches have much larger cavities than in *T. cumingiana*, and the septa at the nodes are not broken through. On examining the surfaces of the branches, each internode is seen to be surrounded near its distal end by a circle of lenticels, and one of

these, for some unknown reason, often becomes considerably enlarged and bears a long, slit-shaped impression. It is in this impression that the queen ant makes the circular perforation that permits her to enter and take possession of the internodal cavity. This recalls the conditions in *Cecropia*, and suggests that ants may be able, through their extremely delicate tactile (or rather chordotonal) sense-organs, to select for perforation the thinnest spot in the wall of a cavity. The cavities in the branches of *T. macombii* are occupied by several species of ants belonging to the genera *Crematogaster, Pheidole, Tapinoma*, and *Iridomyrmex*, but two species are especially common, a small black, narrow-headed *Azteca*, and the black *Pseudomyrma sericea* Mayr. Colonies of all of these species may be found nesting in the internodes of the same branch, but the *Pseudomyrma* is the most abundant and aggressive. It stings quite as severely as its congeners on the acacias, but, unlike the *Ps. arboris-sanctæ* of *Triplaris cumingiana*, it does not take possession of the whole tree, to the exclusion of other species. It is, moreover, a common ant in the hollow twigs of many different trees. As *T. macombii* is a large, vigorous tree, with coarse leaves that can hardly tempt the leaf-cutters, I fail to see how it derives any benefit from its motley assortment of ant-tenants. But that the ants find the hollow internodes of the *Triplaris* the most suitable of habitations can hardly be doubted.

BIBLIOGRAPHY.

1884–86. Beccari, O., Piante ospitatrici ossia piante formicarie della Malesia e della Papuasia—Malesia, ii., Genova, 1884–86.

1874. Belt, Thomas, The Naturalist in Nicaragua. London, 1874.

1842. Bentham, George, Notes on Mimoseæ, with a Synopsis of species—Lond. Journ. Bot., i., 1842, pp. 503–4.

1900. Buscaloni & Huber, J., Eine neue Theorie der Ameisenpflanzen—Botan. Zentralbl., 1900, Beihefte, pp. 85–8.

1697. Commelin, J., Rariorum plantarum Horti Medici Amstelodamensis Descriptio et Icones. Amstelodami, 1697. Tom. i., p. 209, tab. 107.

1877. Darwin, Fr. On the Glandular Bodies of *Acacia sphærocephala* and *Cecropia peltata* serving as food for ants, with an appendix

on the Nectar-glands of the common brake fern, *Pteris aquilina* —Linn. Soc. Journ. Botan., xv., 1877, pp. 398–409, 1 pl.

1874. DELPINO, F., Raporto tra insetti e nettarii estranuziali in alcune piante, 1874.

1886–89. IDEM, Funzione Mirmecofila nel Regno Vegetale—Mem. Accad. Sc. Ist. Bologna, vii., 1886, pp. 215–392; viii., 1887, pp. 601–59; x., 1889, pp. 115–47.

1887–88. IDEM, Weitere Bemerkungen über myrmecophile Pflanzen—Monatl. Mitth. Gesammtgeb. Naturwiss. Herausg., v. E. Huth, 5 Jahrg., No. 2, pp. 25–6, 1887–8.

1891. EMERY, CARLO, Zur Biologie der Ameisen—Biolog. Centralbl., xi., 1891, pp. 165–80.

1892. IDEM, Estudio Contributivo à la Biologia de las Hormigas—Anales. Mus. Nac. Costa Rica (1888–9), pp. 65–7, 1892.

1894. IDEM, Estudios sobre las Hormigas de Costa Rica. I. Hormigas Recogidas en 1889 por Anastasio Alfaro—Anales Mus. Nac. Costa Rica (1889), 1894, pp. 45–64, 2 pls.

1896. IDEM, Formiciden, gesammelt in Paraguay von Dr. J. Bohls—Zool. Jahrb. Abth. Syst., ix., 1896, pp. 625–38, 6 figs.

1889. IDEM, Alleanze Difensive tra Piante e Formiche—Nuova Antologia, ser. iii., vol. xix., 1889, 16 pp.

1909. ESCHERICH, K., Ameisen und Pflanzen—Tharandt. Forst. Jahrb., lx., pp. 66–96, 2 figs.

1909. FIEBRIG, K., *Cecropia peltata* und ihr Verhältnis zu Azteca Alfari, zu Atta sexdens und anderen Insekten, mit einer Notiz über Ameisen-Dornen bei *Acacia catenia*. Ein Kritischer Beitrag zur Ameisenpflanzen-Hypothese—Biol. Centralbl., xxix., 1909, pp. 1–16, 33–55, 65–79, 5 pls.

1892. FOREL, AUG., Die Akazien-Cremastogaster von Prof. Keller aus Somaliland—Zool. Anzeig., xv., 1892, pp. 140–3.

1898. IDEM, La Parabiose chez les Fourmis—Bull. Soc. Vaud. Sc. Nat., xxxiv., 1898, pp. 380–4.

1896. HEIM, DR., The Biologic Relations between Plants and Ants—Smithson. Report, 1896, pp. 411–55, 6 pls. (Transl. from Compt. Rend., 24me Sess. de l'Assoc. Franc. p. l'Advan. Sci., 1895, Ie partie, pp. 31–75.)

1651. HERNANDEZ, F., Nova Plantarum, Animalium et Mineralium Mexicanorum Historia, compilata, deinde a Nardo Antonio. Recchio in volumine digesta. Romæ, 1651.

1886. HUTH, E., Ameisen als Pflanzenschutz. Verzeichniss der bisher bekannten myrmekophilen Pflanzen. Berlin, 1886.

1887. IDEM, Myrmekophile und myrmekophobe Pflanzen—Monatl. Mitth. Gesammtgeb. Naturwiss. 1887, Heft 11–2.

1888. IDEM, Neue myrmekophile Pflanzen—Monatl. Mitth. Gesammtgeb. Naturwiss., 5 Bd., 1888, pp. 219–20.

1907. VON IHERING, H., Die Cecropien und ihre Schutzameisen—Engler's Botan. Jahrb., xxxix., 1907, pp. 666–714, 5 pls., 1 text fig.

1763. JACQUIN, N. J., Selectarum Stirpium Americanarum Historia. Vindobonæ, 1763.
1886. KARSTEN, H., Ameisenpflanzen—Flora, lxix., 1886, pp. 304–6.
1892. KELLER, C., Neue Beobachtungen über Symbiose zwischen Ameisen und Akazien—Zool. Anzeig., xv., 1892, pp. 137–43.
1879. KERNER VON MARILAUN, ANTON, Die Schutzmittel der Blüten gegen unberufene Gäste. Innsbruck, 1879.
1896–98. IDEM, Pflanzenleben, 2 Bd. Leipzig, 1896–1898.
1770. LINNÉ, C., Systema Naturæ, ed. decima tertia, tom. ii., 1770.
1912. MANN, WM. M., Parabiosis in Brazilian Ants—Psyche, xix., 1912, pp. 36–41.
1844. MENEGHINI, G., and SAVI, P., Sulle appendici apiculari proprie alle foglioline dell' Acacia cornigera—Giorn. Botan. Italiano, i., 1844, pp. 106–12.
1911. MIEHE, H., Javanische Studien—Abh. Math. Phys. Kl. Kgl. Sächs. Gesell. Wiss., xxxii., No. 4, 1911.
1911. IDEM, Ueber die javanische Myrmecodia und die Beziehung zu ihren Ameisen—Biol. Centralbl., xxxi., 1911, pp. 733–8.
1720. PLUKENET, L., Opera Omnia Botanica. Lundini, 1720.
1898. VON RACIBORSKY, M., Biologische Mitteilungen aus Java—Flora, 1898, pp. 325–61, 14 figs.
1900. IDEM, Ueber myrmekophile Pflanzen—Flora, 1900, pp. 38–45, 6 figs.
1876. REINKE, J., Beiträge zur Anatomie der an Laubblättern, etc., vorkommenden Secretionsorgane—Pringsheim's Jahrb. f. Wiss. Botan., x., 1876, pp. 117–77.
1904. RETTIG, ERNST, Ameisenpflanzen—Pflanzenameisen. Ein Beitrag zur Kenntnis der von Ameisen bewohnten Pflanzen und der Beziehungen zwischen beiden—Beiheft. Botan. Centralbl., xvii., 1904, 34 pp.
1888. SCHIMPER, A. F. W., Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika—Botan. Mittheil. aus den Tropen., Heft 1. Jena, Gustav Fischer, 1888, 95 pp., 3 pls.
1830. SCHLECHTENDAL and CHAMISSO, Plantarum Mexicanarum a cel. viris Schiede et Deppe Collectarum—Linnæa, v., 1830, pp. 554–625.
1908. SJÖSTEDT, YNGVE, Akaziengallen und Ameisen auf den Ostafrikanischen Steppen—In wiss. Ergeb. Schwed. Zool. Exped. nach dem Kilimandjaro, dem Meru, etc., Uppsala, 1908, pp. 97–118, 3 pls.
1883. TREUB, M., Sur la Myrmecodia echinata de Java—Ann. Jard. Bot. Buitenzorg, 1883.
1888. IDEM, Nouvelles Recherches sur la Myrmecodia de Java—Ann. Jard. Bot. Buitenzorg, vii., 1888.
1907. VON ÜXKÜLL-GÜLDENBRANDT, M. NIEWENHUIS, Extraflorale Zuckerausscheidungen und Ameisenschutz—Ann. Jard. Bot. Buitenzorg, xxi., 2 ser., vi., 1907, pp. 195–327, 10 pls.

1892. WARBURG, O., Ueber Ameisenpflanzen (Myrmekophyten)—Biol. Centralbl., xii., 1892, pp. 129–42.
1806. WILLDENOW, Species Plantarum, tom. iv., pars II, 1806.
1907. WHEELER, W. M., The Ants of Porto Rico and the Virgin Islands—Bull. Amer. Mus. Nat. Hist., xxiv., 1907, pp. 117–58, 2 pls.
1910. IDEM, Ants, their Structure, Development, and Behavior. Columb. Univ. Press, 1910.